

HEAT TOLERANCE AND TEMPERATURE RELATIONSHIPS OF THE FIDDLER CRAB, *UCA PUGILATOR*, WITH REFERENCE TO BODY COLORATION

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Fiddler crabs, *Uca*, being inhabitants of the littoral zone, offer a ready opportunity for study of physiological adaptations associated with the intermediate step in the migration of crustaceans from an aquatic to a terrestrial habitat. Poikilotherms, in general, that have left the aquatic environment require, among others, adequate mechanisms to survive greater extremes of temperature than they had experienced previously. Fiddler crabs are generally active and feeding about the time of low tide. Consequently, when low tide occurs in the middle of the day during the warmer months of the year fiddler crabs on open beaches are exposed to temperatures that are near the lethal level because of the direct solar radiation (Teal, 1958).

The fiddler crab, *Uca pugilator*, exhibits a daily rhythm of color change (Abramowitz, 1937). Specimens are darker during the daytime than at night because the chromatophoral pigments are more dispersed. Brown and Sandeen (1948), working with the same species, found that during the day phase of the rhythm the black pigment tends to concentrate as the temperature rises above 15° C. but the white pigment tends to disperse even further as the temperature increases above 20° C. These responses, which are superimposed on the daily rhythm, would appear to have a thermoregulatory function because during intense sunlight concentration of black pigment would diminish the area which maximally absorbs radiant energy, whereas dispersion of the white pigment would increase the area which reflects this radiation. However, on no crustacean have reflectance measurements been actually performed. Furthermore, no investigator has compared body temperature of pale and dark crustaceans.

Fiddler crabs have been used in a few temperature tolerance studies, but Edney (1961) is the only other investigator who has measured their body temperatures under experimental conditions. Orr (1955) reported the time required to kill all the crabs, *Uca pugilator*, at each of several different temperatures. Teal (1958) determined the upper temperature that was lethal to 50% of the specimens from each of three species of fiddler crabs, *Uca pugilator*, *U. minax*, and *U. pugnax*. The values were 39.5°, 39.9°, and 40.0° C., respectively, but the differences were not statistically significant. Vernberg and Tashian (1959) reported that a tropical zone species, *Uca rapax*, was more resistant to temperatures of 42° and 44° C. than was a temperate zone species, *Uca pugnax*. Edney (1961), who studied the water and heat relationships of five species of *Uca* from Mozambique, found that

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those species from which water transpired faster generally had the lower body temperatures.

The general purpose of the present investigation was to provide further information about the thermal and water relationships of the fiddler crab, *Uca pugilator*. The specific aims were to determine (a) the effect humidity has on body temperature and survival at high temperatures, (b) the influence of body coloration on body temperature, and (c) the rates of transpiration at high temperatures.

MATERIALS AND METHODS

Adult male and female specimens of *Uca pugilator* were collected for use in these experiments at Grand Isle, Louisiana, and at three locations in the area of Woods Hole, Massachusetts; namely, Chapoquoit Beach, Great Sippewissett Creek, and Great Lake. Crabs from Grand Isle were used only for the reflectance study described below. The crabs were maintained in the laboratory in wooden tubs and stainless steel tanks containing sea water. Each container was inclined so that the bottom was not completely covered with water. The sea water was changed every second or third day. The crabs were fed fish which had been cut into small pieces.

To determine the heat death point in saturated air, 10 crabs were placed into each of six 500-ml. Erlenmeyer flasks containing 20 ml. of sea water. Aside from their legs a very small percentage of the body of each crab was in contact with the water. Crabs were chosen without regard to sex because in a preliminary series of experiments no difference between the resistance of the sexes was apparent. The temperature of the water was at the desired value before the crabs were put in. The flasks containing the crabs were quickly immersed completely for one hour in one of a series of constant temperature water baths maintained at the desired temperature. The air above the heated water was ascertained to be 98–100% saturated by directing a stream of air from the flasks over a wet-dry bulb hygrometer suspended in a plastic tube 4 cm. in diameter. After the hour the crabs were removed from the flasks, placed into glass fingerbowls containing sea water, and allowed to stand at room temperature for 12 hours, at which time the number of survivors was ascertained. Any crab which was unable to right itself was not considered a survivor.

Determinations of thermal death limits in dry air were performed through use of an apparatus adapted from the one described by Edney (1951a). This apparatus also allowed determination of transpiration rates. Since surface area was important in the measurement of transpiration, only males were used in this particular set of experiments. Ten crabs were subjected simultaneously to a stream of slowly moving air at a constant predetermined temperature. The air which displaced one liter of water per minute from an inverted graduated cylinder was dried by passage through two chambers of Indicating Drierite. The procedure was performed at six different temperatures.

When body temperatures were determined, as during exposure to sunlight in the habitat, crabs were suspended just high enough over a white sand background so that their legs could not touch the substrate. Each crab was held in position by a tin clamp which gripped it at the lateral edges of the cephalothorax. The clamp was designed to shield a minimal area of the dorsal surface. Body temperatures were measured by means of a Brown Portable Potentiometer (Model 126W2)

modified to supply eight leads and thermocouples of fine gauge copper and constantan wires. The thermocouples were forced into the crabs at the ventral junction of the cephalothorax and abdomen to a position near the midgut.

The specific reflectance of visible light was determined for pale and dark crabs through use of a General Electric Recording Spectrophotometer. The courtesy of the personnel at the Southern Utilization Research and Development Laboratory of the U. S. Department of Agriculture, New Orleans, Louisiana, in making this apparatus available is gratefully acknowledged.

To determine the effect of transpiration alone on the body temperature, crabs in an apparatus adapted from Edney (1951b) were exposed to a stream of slowly moving air of constant temperature which displaced one liter of water per minute. The relative humidity of the air could be adjusted to 0%, 50%, and 100% saturation by passing it through a single chamber or a combination of chambers each containing Drierite, water, or a sulfuric acid solution (Solomon, 1951). The apparatus, including the humidity control chambers, was immersed in a constant temperature bath for each determination. The crabs used in this experiment were clamped in such a position that they were unable to touch the sides of the apparatus.

The rate of transpiration at each of a series of constant temperatures was determined with male crabs each weighing more than two grams through use of the apparatus described above. All crabs were blotted and weighed at the start and weighed one hour later at the completion of the experiment. Data for crabs that defecated during the course of the experiment were discarded. The rate of water loss due to evaporation was expressed as milligrams of water lost per square centimeter of surface area per hour. Surface area was determined by flattening the exoskeletons of a number of weighed crabs, tracing the outlines, and determining their total areas with a planimeter. Then through use of the equation $S = KW^{2/3}$ (Wigglesworth, 1945) a constant could be determined for use with the experimental crabs. The "k" value of adult males was found to be 10.56.

EXPERIMENTS AND RESULTS

Thermal tolerance in dry and saturated air

Groups of crabs were exposed in the manner described above to one of six constant temperatures ranging from 37° to 42° C. in saturated air, and to one of six constant temperatures ranging from 40° to 47° C. in dry air. The experiment with saturated air was performed with a total of 50 crabs at each temperature and in dry air with a total of 20 crabs at each temperature. The percentage survival at each temperature for both groups of crabs is plotted in Figure 1. These experiments were performed during the first two weeks of August, 1960. The temperatures lethal to 50% of the crabs in saturated and dry air are indicated by the dashed lines in Figure 1: 40.7° C. and 45.1° C., respectively. This appreciable increase of the lethal temperature would be expected if crabs in dry air are able to maintain a body temperature below that of crabs in saturated air where transpiration cannot occur. Most of the water loss must have been from the gill surfaces and gill chambers. The lethal temperature for crabs in the field would be expected to lie between the values determined in saturated and dry air and would certainly be approached on hot, clear days.

Effect of humidity on body temperatures

Crabs were exposed in the laboratory first to dry air, then air 50% saturated, and finally fully saturated air. The air temperature was 37.5° C. Air and body temperatures were recorded every five minutes. The humidity was not changed until the body temperature remained constant for 20 minutes. The results are shown in Figure 2. This experiment was performed 21 times. Inspection of the figure reveals a direct proportional relationship between the increase in body temperature at equilibrium and the increase in relative humidity.

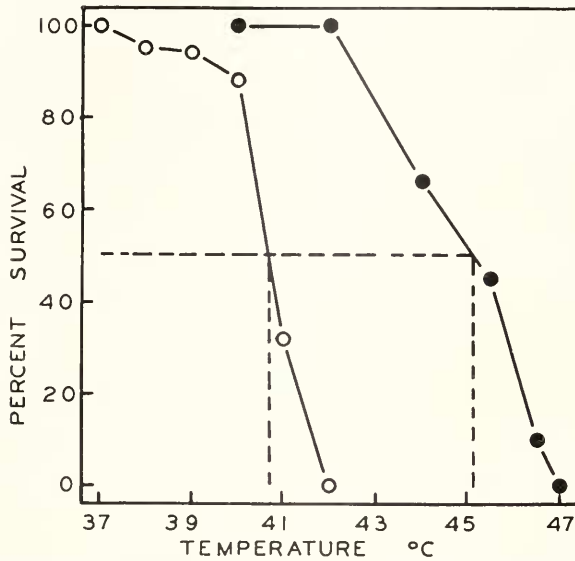


FIGURE 1. Relationships between the temperature to which fiddler crabs were exposed for one hour in saturated air (circles) and in dry air (dots) and the percentage surviving.

In Figure 3 are shown (a) the mean rates of transpiration of water from male crabs in dry air from 28° to 48° C., and (b) the saturation deficit of dry air at each of the experimental temperatures. At each temperature the rate of transpiration was determined for each of 20 crabs. The saturation deficit values were taken from the Handbook of Chemistry and Physics, Fourth Edition. The increase in rate of evaporation with increase in temperature is proportional to the saturation deficit of the air. The similarity of the curves shows that transpiration of water from these fiddler crabs is a physical process completely dependent on the saturation deficit. The crabs apparently have no control over the rate at any temperature.

Effect of coloration on body temperature

This experiment was devised to test the hypothesis that the blanching of fiddler crabs at high temperatures, first described by Brown and Sandeen (1948), has thermoregulatory significance. Dark crabs having maximally dispersed melanin and pale ones with maximally concentrated melanin were taken from the laboratory

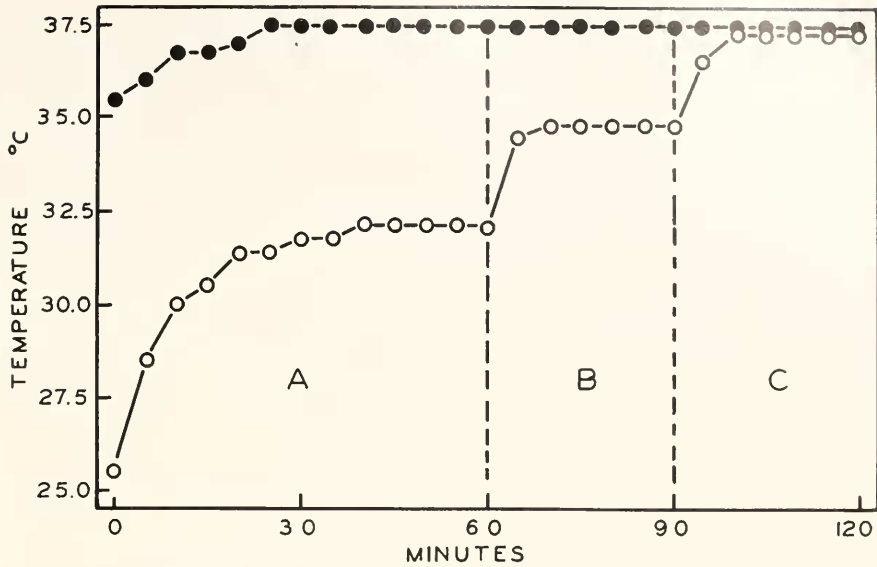


FIGURE 2. Relationship between mean body temperature of crabs and time of exposure to slowly moving air of (A) 0%, (B) 50%, and (C) 100% relative humidity (circles). Air temperature is indicated by the dots.

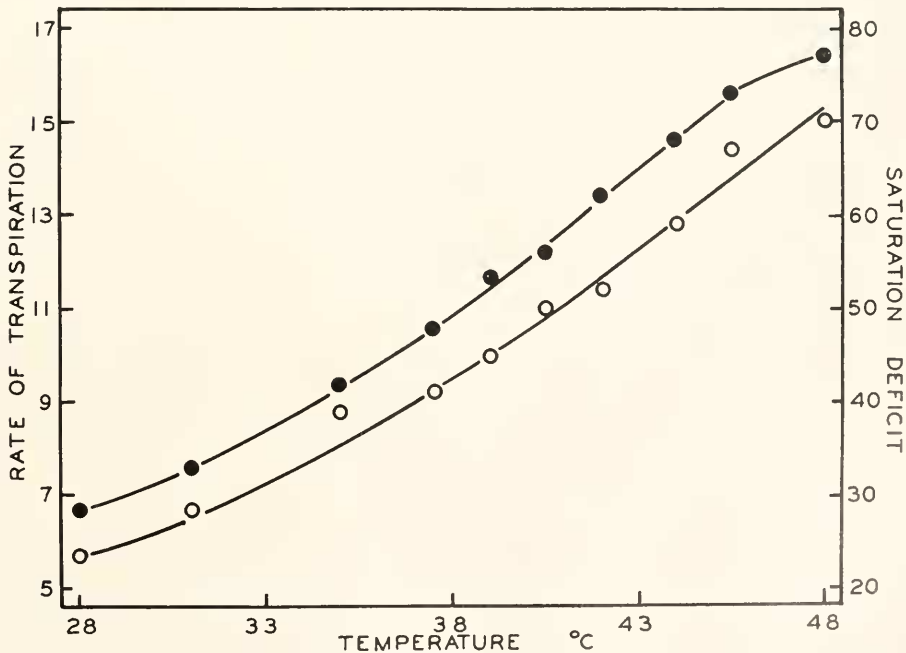


FIGURE 3. Relationships between (a) rate of transpiration from fiddler crabs (mg./cm.²/hr.) and temperature (circles) and (b) saturation deficit (mm. Hg) of dry air and temperature (dots).

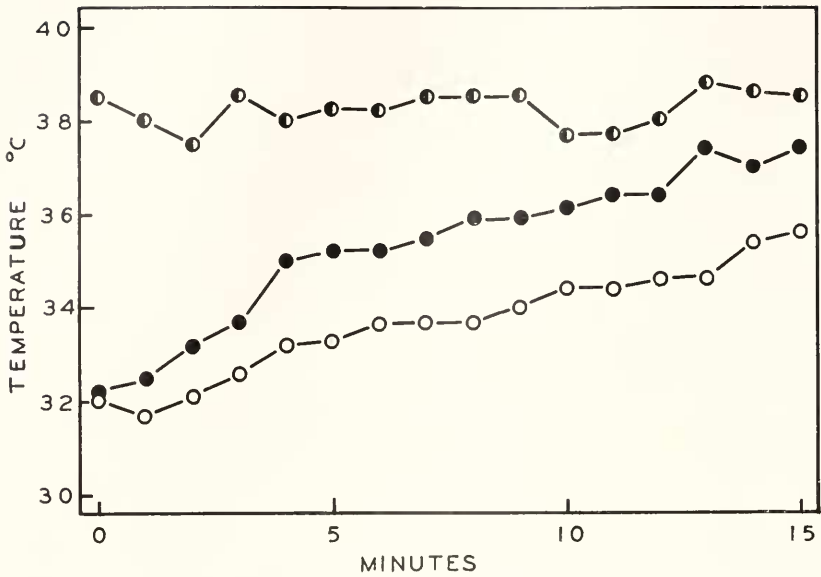


FIGURE 4. Relationships between body temperature of pale (circles) and dark (dots) fiddler crabs and time of exposure to sunlight. Substrate temperature is indicated by the half-filled circles.

and exposed to sunlight on a bright, almost windless day. Their body temperatures were recorded over an interval of 15 minutes while they were clamped in position. The data are presented in Figure 4 where each point represents the mean of 10 determinations. The effect of color differences in absorbing and reflecting radiant

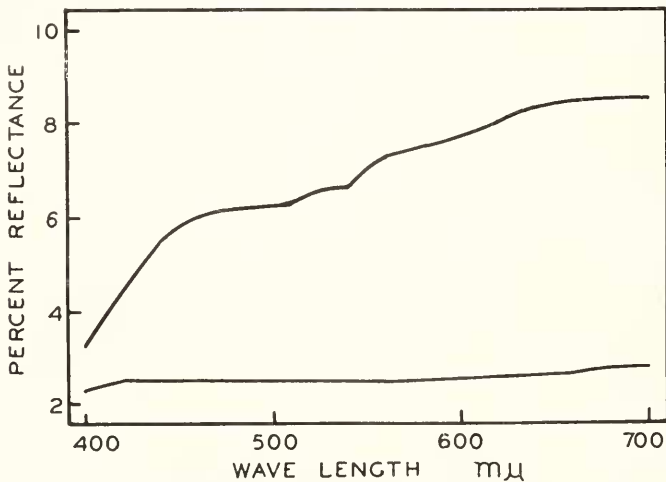


FIGURE 5. Relationships between percentage of light reflected from the dorsal surface of the cephalothorax of pale (upper curve) and dark (lower curve) crabs and the wave-length of light.

energy and converting it to heat is evident in the difference between the rates of heat gain of the pale and dark crabs. Within five minutes after the crabs had been set in sunlight the dark crabs had a body temperature 2° C. higher than that of the pale crabs.

At each of several wave-lengths of visible light from 400 to 700 $m\mu$, the quantity of light reflected from the dorsal surface of the cephalothorax was greater with pale crabs than dark ones (Fig. 5). The difference at the longer wave-lengths was as much as 5%. Furthermore, for both the pale and dark crabs the percentage of light reflected was greater at the longer wave-lengths than at the shorter ones although the contrast between the shorter and longer wave-lengths was more readily apparent with pale crabs than with dark ones.

Observations of field behavior of specimens of Uca pugilator

Field observations of the activity and behavior of natural populations of *Uca pugilator* were made throughout July and August, 1960, at Chapoquoit Beach and Great Sippewissett Creek. Observations of individual crabs were made from a distance through binoculars. The days chosen were clear and hot with a minimum of wind (1 on the Beaufort scale; direction of wind shown by smoke drift only. Meteorological Observer's Handbook, 1942). The air temperature averaged 27.5° C. at a height of 2 cm. above the ground. The surface, dry sand, averaged 42.5° C. The air temperature in burrows in this dry sand 2 cm. below the surface averaged 30° C. and 15 cm. below the surface was 26° C. Excavation revealed that all burrows ended in very damp or wet sand. The average relative humidity on the days of observation was 60%, determined with a sling psychrometer held 60 cm. above the surface.

On hot days crabs were observed actively feeding predominantly in areas where the surface of the sand was still moist; however, occasionally they were also active on the drier parts of the beaches. In their normal course of activity the crabs would feed for a while and then retreat into their burrows. It was observed that each crab would feed for 15 to 20 minutes at a time, then disappear into a burrow for three or four minutes and reappear to resume feeding. Therefore, the frequency of this "feeding-retreat" rhythm is 18-24 minutes. The crabs did not enter their burrows *en masse* as they do when startled, but each individual adhered closely to its own cycle.

DISCUSSION

The lethal temperatures indicated in Figure 1 at which 50% of the crabs died are more meaningful statistics than are the temperatures at which 100% of the crabs died. The latter temperatures must necessarily include even the most resistant individuals. Teal (1958) found that 50% of the fiddler crabs, *Uca pugilator*, that he used died after they had been exposed for one hour to a temperature of 39.5° C. "by placing the animals in enough sea water of the desired temperature so that each animal was slightly more than half covered." The lowest corresponding value found in the present set of experiments was 40.7° C. with crabs in saturated air. This difference is probably a reflection of the difference in experimental technique because in the present experiments 10 crabs and only 20 ml. of sea water were placed

into a 500-ml flask, with the result that very little submergence of the crabs occurred. It will be recalled these flasks were immersed completely in a constant temperature water bath but Teal did not state how he kept the temperature of his flasks constant.

The data presented herein confirm and extend the observations of Edney (1961) on five species of African fiddler crabs. He found, as herein, that (a) the temperature within the burrows during the warmer months of the year is considerably cooler than the sand at the surface, and (b) an appreciable reduction in body temperature occurs as a result of transpiration. The ability to withstand high surface temperatures by transpiration undoubtedly has a significant survival value. The upper lethal temperatures at which all of Edney's crabs died ranged from 42° to 45° C. for the five species after immersion in water of the appropriate temperature for 15 minutes. With one hour of exposure in saturated air the temperature required to kill 100% of the *Uca pugilator* herein was 42° C. which is the same temperature that was lethal to all of Edney's specimens of *Uca marionis*, *U. urvillei*, and *U. chlorophthalmus*. Edney obtained these particular data in January, 1959. Inhaca Island, where he worked, is south of the Equator, rendering January one of the warmer months of the year for these crabs. It was shown herein for the first time with a fiddler crab that (a) the amount of cooling resulting from transpiration is proportional to the decrease in relative humidity (Fig. 2), and (b) the "saturation deficit law" as stated by Edney (1957) is obeyed (Fig. 3).

The results shown in Figure 4 support the hypothesis of Brown and Sandeen (1948) that the blanching of fiddler crabs at high temperatures has a thermoregulatory role. Pale crabs maintained themselves about 2° C. cooler than dark crabs. The measurements of quantities of visible light reflected from pale and dark crabs (Fig. 5) are qualitatively similar to the findings of Deanin and Steggerda (1948) with pale and dark frogs. However, Deanin and Steggerda did not measure the body temperatures of their frogs but they did point out that the greater reflection of light at the red end of the visible spectrum than at the violet end may also have adaptive significance in view of the greater heating capacity of the rays having the longer wave-lengths.

The observation that fiddler crabs cease feeding and enter their burrows every 18-24 minutes can be interpreted as a behavioral mechanism for control of body temperature. Every time a crab descends into its burrow the escape from sunlight to the cooler air would allow the body temperature to decrease several degrees.

Palmer (1962), working with a different species of fiddler crab, *Uca pugilator*, found a daily phototactic rhythm; the crabs spent a greater proportion of time in the illuminated end of the apparatus during the morning hours than at other times of day. An attempt at thermoregulation may in part underlie the change in strength of phototaxis because between 5 and 8 AM, when the crabs show a strong positive response to light, the air is usually cool, but during the warmer portion of the day the attraction to light, hence the tendency to leave the burrows, is not so great.

SUMMARY AND CONCLUSIONS

1. Upper thermal death points were determined for the fiddler crab, *Uca pugilator*. In saturated air the lethal temperature for 50% of the crabs, determined

graphically from the experimental data, after an exposure of one hour, was 40.7° C. All of the crabs died after one hour at 42° C. In dry air the corresponding temperatures were 45.1° C. and 47° C. for the same time of exposure.

2. Five minutes after having been placed in sunlight the body temperature of dark crabs was 2° C. higher than that of pale crabs. More visible light is reflected from the dorsal surface of the cephalothorax of a pale crab than from a dark crab. The difference is more striking with the rays of longer wave-length which have a greater heating capacity than the rays at the violet end of the visible spectrum. These observations support the hypothesis that the blanching that occurs at high temperatures has a thermoregulatory role.

3. The body temperatures of crabs maintained either in dry air or in air having a relative humidity of 50% were lower than the air temperature, undoubtedly due to transpiration of water. The body temperatures of crabs in saturated air were the same as the air temperature. The cooling that resulted from transpiration was proportional to the decrease in relative humidity.

4. Transpiration from this crab is a passive process. The rate is proportional to the saturation deficit of the air.

5. In their habitat specimens of *Uca pugilator* exhibit a "feeding-retreat" rhythm that has a frequency of 18-24 minutes. There is no phase interaction between individuals in a population. On hot days the frequent periodic return to the cooler burrows can serve to lower the body temperature.

6. These findings were discussed in relation to the observations of other investigators.

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